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26 Bobwhite

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Bobwhite

Colinus virginianus (Linnaeus) 1758

OTHER VERNACULAR NAMES

AMERICAN colin, Codorniz Común, Cuiche Común, partridge, quail.

RANGE

Virtually all of the eastern United States north to southern Maine, New York, southern Ontario, central Wisconsin, and central Minnesota, west to southeastern Wyoming, eastern Colorado, eastern New Mexico, and eastern Mexico south to Chiapas and adjacent Guatemala, but excluding the lowlands of Yucatán. Also existing as isolated populations in Sonora (largely extirpated) and as introduced populations in the Columbia and Snake river basins of Washington, Oregon, Idaho, and northwestern Wyoming (Bighorn and Shoshone river valleys). Currently being reintroduced into southern Arizona.

SUBSPECIES (*ex A.O.U. Check-list* and Aldrich, 1946; Mexican Races from *Check-list of Birds of Mexico*)

C. v. virginianus: Eastern bobwhite. Resident of the southern Atlantic

seaboard north to Virginia southwest to north central Georgia, southeastern Alabama, and northern Florida.

C. v. marilandicus (Linnaeus): New England bobwhite. Resident of New England north to southwestern Maine southwest to east central New York, Pennsylvania, and central Virginia and south to southern Maryland and Delaware (not in *A.O.U. Check-list;* part of *C. v. virginianus*).

C. v. mexicanus (Linnaeus): Interior bobwhite. Resident of much of eastern United States east of the Great Plains excepting the Atlantic Coast (not in *A.O.U. Check-list;* part of *C. v. virginianus*).

C. v. floridanus (Coues): Florida bobwhite. Resident of most of peninsular Florida.

C. v. texanus (Lawrence): Texas bobwhite. Resident of most of southern Texas adjacent to New Mexico and northern Mexico including parts of Coahuila, Nuevo León, and Tamaulipas.

C. v. taylori Lincoln: Plains bobwhite. Resident of the Great Plains from South Dakota southward to northern Texas and eastward to western Missouri and northwestern Arkansas. Introduced populations in Washington, Oregon, and Idaho in the Columbia and Snake river basins.

C. v. ridgwayi Brewster: Masked bobwhite. Resident in central interior Sonora and formerly north to southern Arizona. The fate of recent Arizona restocks (near Arivaca and in Altar Valley) is still uncertain.

C. v. cubanensis (Gray): Cuban bobwhite. Resident in Cuba and the Isle of Pines.

C. v. maculatus Nelson: Mottled or spotted-bellied bobwhite. Resident from central Tamaulipas south to northern Veracruz and west to southeastern San Luis Potosí.

C. v. aridus Aldrich: Jaumave bobwhite. Resident from the northern part of southeastern San Luis Potosi to central and central western Tamaulipas.

C. v. graysoni (Lawrence): Grayson bobwhite. Resident from southeastern Nayarit and southern Jalisco on the Mexican tableland south to the Valley of Mexico, Morelos, southern Hidalgo, and central southern San Luis Potosí.

C. v. nigripectus Nelson: Puebla bobwhite. Resident in the plains of Puebla, Morelos, and Mexico.

C. v. pectoralis (Gould): Black-breasted bobwhite. Resident in central Veracruz at elevations of from five hundred to five thousand feet along the eastern base of the Cordillera.

C. v. godmani Nelson: Godman bobwhite. Resident in the lowlands of Veracruz from sea level to fifteen hundred feet and intergrading with *minor* in Tabasco.

C. v. minor Nelson: Least bobwhite. Resident on grassy plains of northeastern Chiapas and adjacent Tabasco.

C. v. insignis Nelson: Guatemalan bobwhite. Resident in the valley of the Río Chiapas (Río Grijalva) in southern Chiapas and adjacent Guatemala.

C. v. coyolcos (Müller): Coyolcos bobwhite. Resident along the Pacific coast of Oaxaca and Chiapas in the vicinity of the Gulf of Tehuantepec.

C. v. salvini Nelson: Salvin bobwhite. Known only from the coastal plains of southern Chiapas near the Guatemalan border.

C. v. thayeri Bangs and Peters: Thayer bobwhite. Resident in northeastern Oaxaca.

C. v. atriceps (Ogilvie-Grant): Black-headed bobwhite. Resident from the interior of western Oaxaca (Putla) northward along the coast to central Guerrero (Acapulco) and probably south to the range of *harrisoni.*

C. v. nelsoni Brodkorb: Nelson bobwhite. Known only from extreme southern Chiapas; of doubtful validity (Edwards and Lea, 1955).

C. v. harrisoni Orr and Webster. Recently described (1968) from southwestern Oaxaca near the coastal plain.

MEASUREMENTS

Folded wing (United States forms): Adults, both sexes, 98-119 mm (sexual differences negligible).

Tail (United States forms): Adults, both sexes, 49-70 mm (males average 3 mm longer than females).

IDENTIFICATION

Length, 9.5–10.6 inches. The sexes are very different in appearance, and males vary greatly in coloration in different parts of the species' range. Males of most races, however, have a white eye-stripe that extends from the bill through the eye back to the base of the neck, with brown to brownish black coloration above. The ear region is blackish to hazel brown in males, and this feathering extends backward below the white eye-stripe and expands under the throat to form a blackish chest collar under the white chin and throat of most races. However, in some populations the chin and throat are also black, and the lower chest may be either blackish or brownish. In the northern populations the breast and abdomen are irregularly barred with black and white in males, but in southern Mexico all underparts are generally darker and lack white markings. Females of all races have buffy chins, upper throats, and eye-stripes, and buffy tones likewise replace the white

underpart coloration of males. Females also lack black collars and in general are more heavily marked with brown and buff barring or mottling both above and below.

FIELD MARKS

Except in some parts of Mexico, the presence of a white throat and a white eye-stripe that contrasts with an otherwise brownish to blackish head will serve to identify male bobwhites. Likewise, no distinct crest is present in this species. Bobwhites most closely resemble the black-throated bobwhites of the Yucatán peninsula but are geographically isolated from them. Gray partridges might be confused with bobwhites, but the gray partridge has no white or pale buff on the head and also has a uniformly grayish chest. The whistled *bobwhite* location call of males in spring is distinctive (but also occurs in the next species), and similar whistled notes serve as separation calls in reassembling scattered coveys.

AGE AND SEX CRITERIA

Females have buffy chins and upper throats, as compared with the white (black in *ridgwayi* and some Mexican races) chins and upper throats of males. The whiter chins of males appear to some extent even in the juvenal plumage. The beak coloration (pale yellow present at the base of the lower mandible in females; males uniformly black) is useful in determining sex of birds as early as 6 to 8 weeks old (Loveless, 1958). Sex of birds at least eight weeks old can be determined on the basis of the central portion of the upper middle wing coverts (Thomas, 1969). Males have fine, black, sharply pointed and well differentiated markings here, whereas females have wider, dull gray bands that do not contrast sharply with the rest of the feathers.

Immatures can often be identified by the fact that their outer two primaries are more pointed than the others (Stoddard, 1931), and the upper greater coverts of the first seven primaries have buffy tips (Leopold, 1939). A small percentage of birds may still be of questionable age by these two criteria, in which case first-year birds may be identified by using the seventh upper primary covert, which is usually brownish with buffy tipping and is somewhat ragged. In adults this feather is darker, sleeker, and has more whitish downy tipping at the feather base (Haugen, 1957).

Juveniles have whitish mottling on the tail feathers and the primaries also have mottled buffy edgings. Pale shaft-streaks are also evident on the upperparts, producing a distinctive light over-all coloration.

Downy young (illustrated in color plate 110) of bobwhites may be dis-

tinguished from the *Callipepla* group by their lack of a crest and distinctive spinal stripe and from *Oreortyx* young by their more buffy faces and underparts, as well as their lack of clear black coloration dorsally. The middorsal stripe of bobwhites is russet to chestnut and only slightly darker laterally than in the middle, and the pale stripe immediately below is tinged with brown. A narrow, discontinuous dark stripe extends from the back of the eye to beyond the ear region, where it merges with the darker "shoulder" region. See the black-throated bobwhite account for distinction from that species.

DISTRIBUTION AND HABITAT

The total distributional range of *Colinus virginianus* is a remarkably broad one, extending from the southern part of Maine on the east coast in a nearly unbroken series of populations to the Texas-Mexico border, and southward along the eastern foothills of the Sierra Madre Oriental almost to the Río Usumacinta, and to the Chiapas-Guatemala border in the highlands and Pacific slope. The northern limits of the species' range are extreme southern Maine (Aldrich, 1946; Palmer, 1949), Massachusetts (Ripley, 1957), southern New York (Brown, 1956), southern Ontario (Clarke, 1954), the southern half of Michigan's Lower Peninsula (Janson, 1969), southern Wisconsin (Gromme, 1963), and southern Minnesota, where it is now largely limited to the extreme southeastern part of the state in the Mississippi valley (Longley, 1951).

The western limits of the species' native range are in wooded or brushy river valleys from South Dakota southward along the western limits of mixed-grasses prairies to western Oklahoma and Texas. In Nebraska the bird occurs along wooded river valleys (Platte, Republican, Frenchman) all the way to the Wyoming and Colorado borders (Mohler, 1944; Aldrich, 1946). In eastern Wyoming it is probably native only to the North Platte valley but has recently been well established near the Shoshone and Bighorn rivers in north central Wyoming (Our feathered friends, Wyoming Game and Fish Commission). In eastern Colorado the bobwhite is a local resident all the way west to the edge of the foothills (Bailey and Niedrach, 1967), and in extreme eastern New Mexico the species is largely restricted to the plum thickets or similar low shrubby growth (Ligon, 1961).

In the Oklahoma panhandle the bobwhite is limited largely to river bottom habitats, where tree thickets grow adjacent to pasture lands and relatively dense ground-level cover exists, but it is virtually lacking from the short-grass and sand sage (*Artemisia*) habitats utilized by the scaled quail (Schemnitz, 1964). In western Texas the range extends to about the

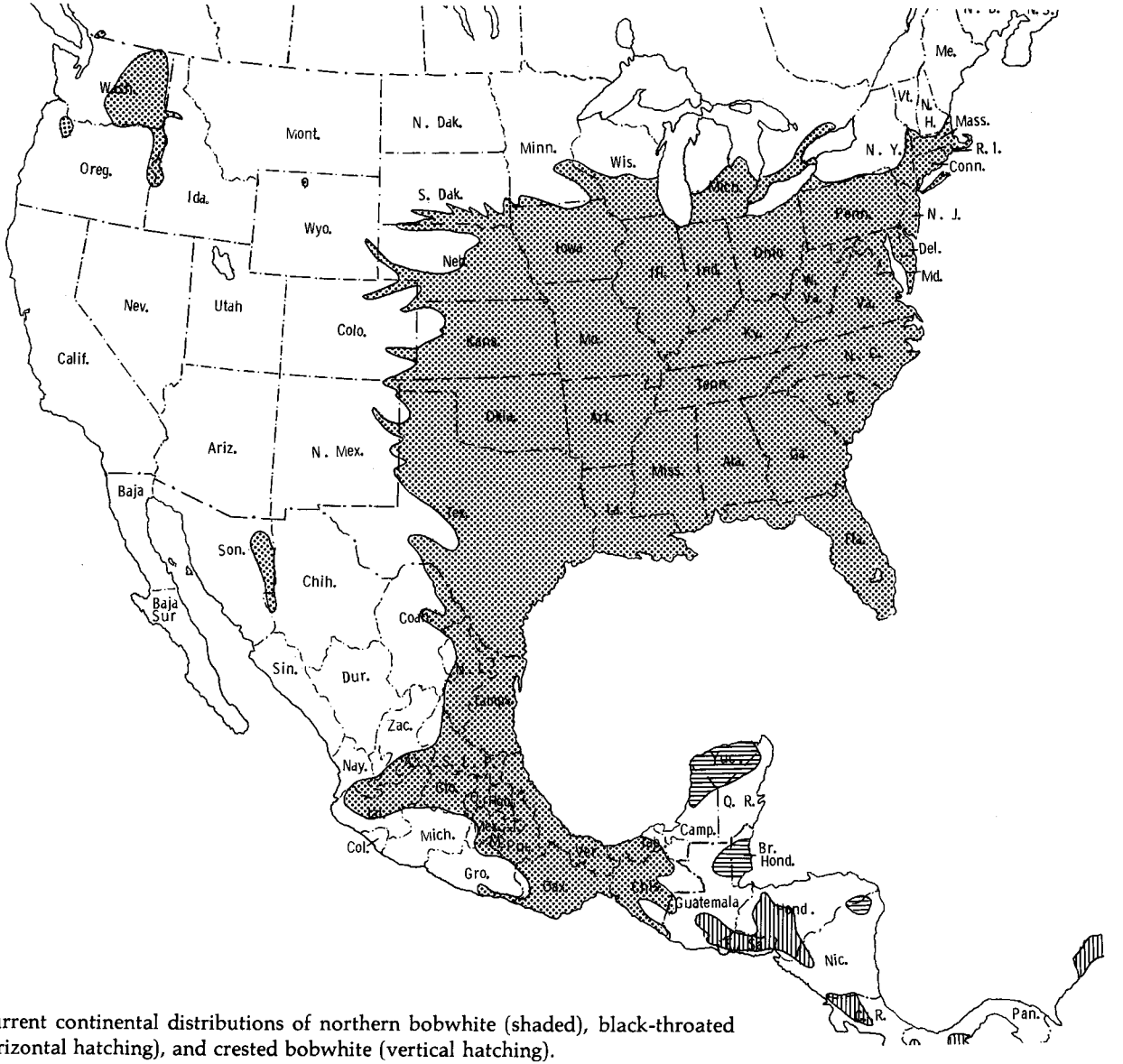

FIGURE 39. Current continental distributions of northern bobwhite (shaded), black-throated bobwhite (horizontal hatching), and crested bobwhite (vertical hatching).

102d meridian; in western and southern Texas the more arid-adapted Texas bobwhite replaces the plains bobwhite, and the birds exist in fair populations wherever excessive grazing does not occur (Principal game birds and mammals of Texas, 1945).

Except for the extirpated Arizona masked bobwhite population (Ligon, 1952), all the more western populations of bobwhites are the result of introductions. In 1970, an attempt to reintroduce the masked bobwhite into southern Arizona was begun by releasing 356 hand-reared offspring of wild birds that had been captured in Sonora during 1968. The success of this effort is still unknown, but well-established populations of bobwhites do occur in Washington, Oregon, and Idaho. In Washington the bobwhite is widely established in the Columbia River basin, and also occurs on a few islands (such as Whidbey) of Puget and Washington sounds, where it was initially introduced in 1871 (Jewett et al., 1953). Birds on the adjoining mainland may barely reach the British Columbia border in the vicinity of Huntingdon. The interior range is more restricted now than formerly, and the bird is presently best surviving in irrigated areas and river valleys such as the Yakima valley (Larrison and Sonnenburg, 1968). In Idaho the bobwhite was first introduced in the Boise valley in 1875, and presently it is found on the lower Boise, Payette, and Weiser river valleys (Upland game birds of Idaho, 1951). In Oregon, where the bobwhite was first released in 1879, the species is best established in the Willamette Valley, as well as near the Columbia River in Morrow and Umatilla counties, and in the Snake River drainage of Malheur County (Masson and Mace, 1962).

The Mexican distribution of the bobwhite has been plotted by Leopold (1959), whose map has been the basis of my own indication of the species' range except the southern parts of Mexico. Further, the present known range of the masked bobwhite in Sonora is much more restricted than is shown by Leopold; it is now believed to be restricted to three small areas there, and the total population may number between four hundred and one thousand birds.

The bobwhite's range in Guerrero has been questionable; Friedmann, Griscom, and Moore (1950) indicate that *atriceps* probably ranges into that state but do not list *nigripectus* for it. Leopold shows only one specimen record for the state, near the Oaxaca boundary, which is presumably referable to *atriceps*. I heard and saw a white-throated male bobwhite calling on the outskirts of Iguala on June 1, 1970, which most probably represented *nigripectus*. From the vicinity of Acapulco southward along the coast toward the Oaxaca border the species is fairly common in brushy habitats. I saw more than thirty in the area near Acapulco and inland as far as Xaltianguis. I also examined several live males that had been captured near Acapulco, and these all had the uniformly dark head color (no superciliary stripe) and a

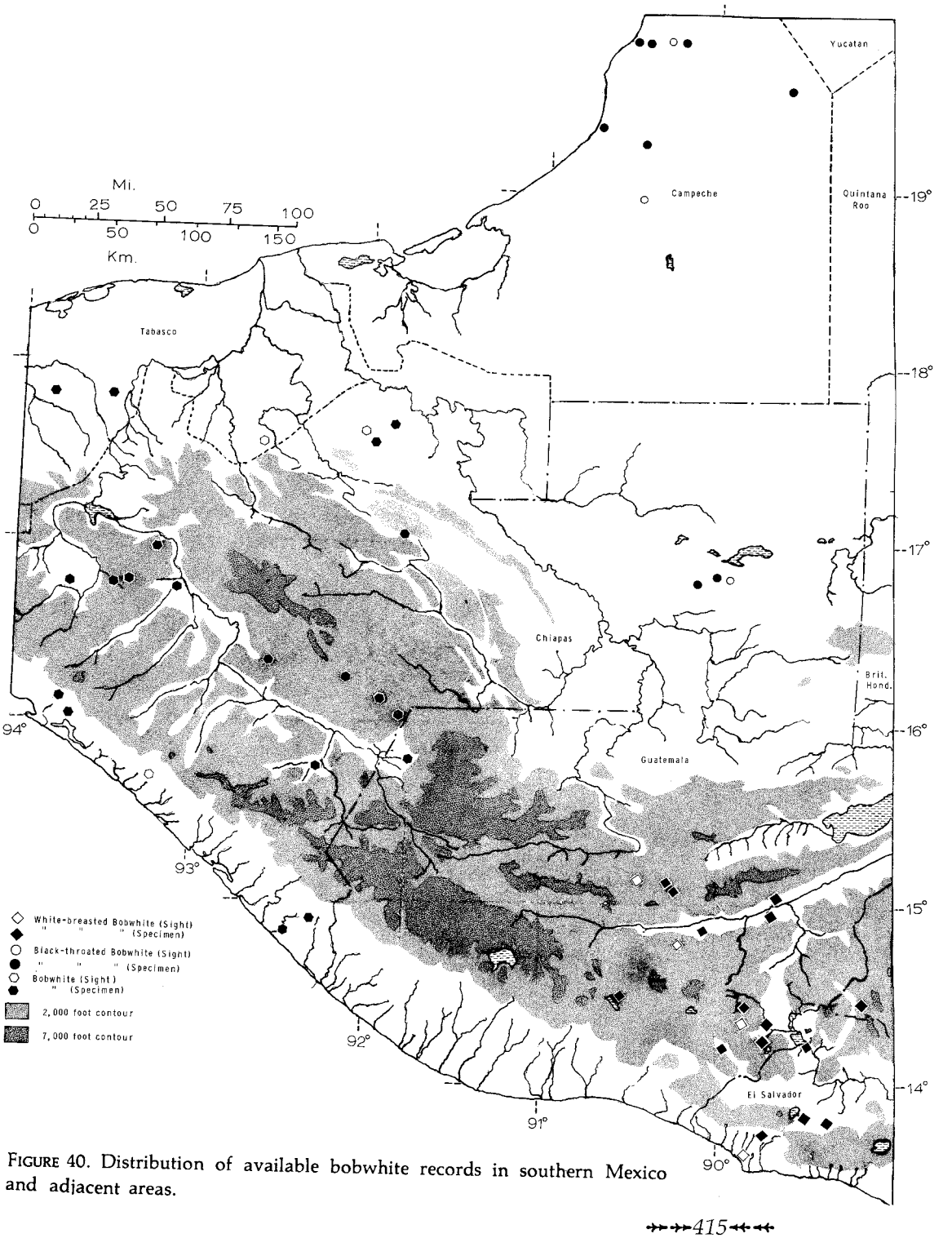

FIGURE 40. Distribution of available bobwhite records in southern Mexico and adjacent areas.

solid black chest, as is typical of *atriceps*. Of two males collected near Xaltianguis, about fifty kilometers inland, one had a slightly light chestnut breast and one had a streaked black and chestnut breast rather than a uniformly black chest, but their heads had no more white present than was typical of the coastal birds. They probably more closely approach the recently described form *harrisoni* (Orr and Webster, 1968), from southwestern Oaxaca. However, I believe that the reduced degree of melanism and resultant plumage similarities shown in the birds from these two areas is of independent origin and simply a reflection of local adaptation to more arid climates.

Although I did not see bobwhites in the vicinity of Copala, Guerrero, I was informed that they occur near there by local residents. Ten miles west of the Guerrero-Oaxaca line near Caljinicuilapa I saw a pair of bobwhites, the male of which appeared to be typical *atriceps*. Another pair was seen along the Río Verde (thirty-one miles southeast of Pinotepa Nacional), and between Pinotepa Nacional and Putla (the type locality of *atriceps*) I saw a total of twenty birds during a single trip. I would judge that Putla represents the interior limit of this subspecies' range, since high and wet country farther to the north is clearly unsuited to bobwhites. Presumably, intergrade populations between *atriceps* and *harrisoni* occur between the Río Verde and San Gabriel Mixtepec, but this road was impassable during the summer of 1970 and thus the area in question could not be visited. Binford (1968) believed that the species occurs along the entire length of the Pacific region of Oaxaca, occurring in savanna and arid tropical scrub habitats, as well as in altered habitats within the general range of tropical deciduous and tropical evergreen forest zones. In the arid interior uplands a white-throated form, *thayeri*, also occurs, and Blake (1950) collected it on the Atlantic drainage near Tutla. In the vicinity of the Gulf of Tehuantepec the coastal population *coyolcos* occurs at least as far west as the town of Tehuantepec. In the Isthmus region the type locality (Chivela) of *thayeri* suggests a population connection with lowland Veracruz bobwhites, but at the eastern edge of the Isthmus and just across the Oaxaca-Chiapas border, specimens referable to *insignis* have been collected on grasslands near Monserrate (Edwards and Lea, 1955). Thus, near the Oaxaca-Chiapas border three rather distinctly different populations probably intergrade, the white-throated race *thayeri*, and the black-throated races *coyolcos* and *insignis*. There is probably a good deal of individual variation in throat and body coloration among birds from this area, judging from remarks made by Ridgway and Friedmann (1946), and many specimens may not be identifiable as to subspecies.

Bobwhites of the race *insignis* are extremely common in the central

plateau of Chiapas; I observed them in numerous locations from the outskirts of Cintalapa to a point a few miles west of the Lagunas de Monte Bello, close to the Guatemala border, and I was told by local hunters that they are abundant in the upper reaches of the Río Chiapa (Río Grijalva) all the way to the Guatemala border. At least four of nearly fifty males which I observed closely had no indication of a white superciliary stripe, thus the trait cannot be regarded as a criterion of this subspecies. The interior limits of *insignis* and the possible intergradation of this race with the white-throated race *minor* remain uncertain. Of five male specimens in the University of California collection that have been collected at El Real, Chiapas, all have black throats, but one (MVZ #98109) has "considerable white in the malar regions and laterally on the throat."* Thus it is possible that there has been limited population contact between these highland populations and the lowland populations of *godmani* and *minor* that occur along the wet Caribbean-facing slopes of Chiapas and Tabasco.

Berrett (1963) reported that bobwhites were commonly observed in open savannas of western Tabasco; specimens he examined from that area were closer to *minor* than to *godmani*. He noted that little suitable habitat for bobwhites occurs between that area and eastern Tabasco in the vicinity of Macuspana. East of Macuspana, just across the Chiapas border, fairly extensive savanna occurs between the Río Usumacinta and the wet forests behind Palenque. This area, which is the type locality of *minor*, still supports bobwhites. I saw several pairs in that vicinity and was told by local residents that the birds are hunted to some extent. It is difficult to be certain whether these savannas are partially of natural origin, but when the forests are removed through burning an excellent growth of tall grasses that are highly suitable for grazing purposes can be attained. Bobwhite habitat is, if anything, improving rather than deteriorating in this area as the incidence of well-managed cattle ranches increases.

POPULATION DENSITY

It has been generally agreed that Leopold (1933) was correct in assigning a maximum (fall) quail density of one bird per acre, which he believed represented a saturation point of the species rather than a carrying capacity of the land. He believed that the area of the species' probable optimum range, which centered on the states of Missouri, Illinois, Indiana, and parts of Iowa, was most likely to support populations that would reach but not exceed the saturation point, and he further noted that populations in the more southern states of Mississippi and Georgia were also known to attain this

*N. K. Johnson, 1969: personal communication.

population density. However, on the northern and western parts of the bobwhite's range the populations tended to fluctuate and along the western border of the species' range its density at times exceeded the saturation point in the judgment of Leopold. He noted one Texas estimate of more than two bobwhites per acre over several sections of land in Kenedy County during 1930. In Texas the highest average breeding densities are attained in sandy mesquite semiprairies, pine-oak woodland with interspersed small farms, and transitional coastal prairie uplands, particularly the semiprairies, where early fall densities are generally one per four or five acres but sometimes up to a bird per acre (Principal game birds and mammals of Texas, 1945).

Edminster (1954) suggested that over the best quail range, fall densities may reach from two to ten acres per quail and from ten to fifty or more acres per bird in marginal range. Spring population densities are approximately half the fall figures, or up to a pair per four acres.

In a Kansas study area of about 640 acres, Robinson (1957) estimated that during 1952 a breeding population of 102 birds (with thirty-six mated pairs) was present, while in 1953 the breeding population was 91 birds (with thirty-two mated pairs). Thus, nesting densities of one nest per 20 acres might be expected from such late spring densities. He estimated the maximum carrying capacities of the land for bobwhites to be fifty-three or fifty-four coveys per section during late autumn, since at least 12 acres of habitat are needed to support a single covey. Because his fall coveys consistently averaged 11 to 13 birds, this would agree with other estimates of about one bird per acre as a maximum fall density. It should be noted, however, that he regarded this maximum density to be determined by the carrying capacity of the land rather than to represent a saturation point determined by the species. A density in excess of one bird per acre has recently been reported by Kellogg, Doster, and Williamson (1970).

HABITAT REQUIREMENTS

Edminster (1954) classified the cover types used by bobwhites into four general groups: grasslands, croplands, brushy habitats, and woodlands. He regarded grasslands to be of value primarily during the spring and summer, when they provide nesting cover, some feeding cover, and limited roosting cover. Croplands receive major use during summer and fall, when they provide feeding, loafing, dusting, and limited roosting sites. Brushy areas and woodlands are used through the year for escape and roosting cover but are vital during fall and winter for feeding. Edminster believed that from 30 to 40 percent of the land area should be in grassland,

40 to 60 percent in crop fields, 5 to 20 percent in brushy cover, and 5 to 40 percent in woodland cover for ideal habitat, with a maximum of habitat interspersion and edge margins between habitat types.

Casey (1965) reviewed previous analyses of bobwhite habitat requirements and concluded that three major vegetative types must be present, including grassy nesting cover, cultivated crops or a similar source of food, and brushy cover. He believed that woodlands are not necessary if a brushy cover equivalent to a woodland understory is present. He further believed that a vital habitat factor is the presence of a brushy or woody covey "headquarters," using the earlier concept proposed by Robinson (1957). Such a headquarters must have protective vegetation to provide loafing cover during midday and be separated by about 140 yards from any other covey headquarters. Robinson has found that among ten such headquarters that were in continuous woody vegetation the mean distance between adjacent headquarters was 138 yards. He suggested that such headquarters should consist of areas at least 15 yards square (225 square yards), although some reports indicate that dense woody clumps as small as six feet in diameter might serve, too.

Roosting cover requirements for bobwhites vary somewhat between summer and winter (Rosene, 1969), with the typical roosting behavior serving in winter to maintain body heat through the use of a disk-like formation of birds oriented with their tails together and bodies touching on both sides. Quail use the same circular formation in summer, too, but then the importance of the formation for heat-retention is reduced. The ideal size of such a roosting disk is ten to fifteen birds, and thus the behavior largely regulates the size of winter coveys, a situation in marked contrast to the southwestern desert quail species. Although coveys much larger than fifteen birds will form two such roosting disks, coveys that become smaller will join with nearby groups to maintain this minimum roosting group size. Rosene noted that in the southeast, good winter roost sites are usually on gentle slopes with good drainage, with herbaceous vegetation about two feet high, with bare ground below and exposed sky above. Similarly, in southern Illinois, the sites selected for roosting were usually on medium to low elevations with good drainage, often with south or southwesterly (rarely east or north) exposures that remained warm late in the afternoon, and on bare ground or ground covered only with duff (Klimstra and Ziccardi, 1963). Associated vegetation was typically herbaceous, averaging fifty-nine centimeters high, with relatively little light obstruction. Wheat stubble cover resulting from combining with associated weedy herbs provided ideal roosting cover, and limited burning or grazing may also improve grassland cover for roosting purposes.

Nesting cover requirements are essentially open herbaceous cover with nearly bare ground. The vegetation is usually under twenty inches high, and the stems are sufficiently far apart for the birds to walk through easily. Dead herbaceous material is needed to make the nest lining; thus areas that were not burned the prior spring are preferred over burned areas. Nests are usually within fifty feet of cover edges or other bare ground situations (Rosene, 1969).

To a much greater extent than is the case with the desert-living quails, water in the form of dew or surface water is needed by bobwhites. In the more arid parts of the species' range, the bobwhite becomes increasingly dependent on irrigated areas, river valleys, or other relatively moist habitats. Finally, like all quail, suitable dusting sites are needed in the form of dry and rather powdery soil. Roadsides, field edges, or burned areas all provide such dusting sites, which the birds may visit daily if weather permits.

FOOD AND FORAGING BEHAVIOR

Literally dozens of papers have been written on the food consumption of bobwhites, and it would be impossible to summarize all of them in the available space. Rosene (1969) has provided a recent summary, and the following discussion is based largely on his review.

The animal portion of the bobwhite's diet varies from about 30 percent in summer to only about 5 percent in winter, with the availability of insects largely determining the incidence of foods from this source. However, in southern Florida, where insects are available the year around, the cycle of insect use is similar, indicating a preferential use of insects according to protein needs, which are highest during the period of reproduction.

Based on a study of 1,400 quail crops obtained in Alabama, Rosene concluded that eight of the fourteen most important plant food items were seeds of legume species, and seeds of all types made up 93 percent of the fall diet. Over 3,000 samples obtained from four different soil-type areas of Alabama indicated some regional differences in food consumption. On the sandy coastal plains soils acorns almost equalled legumes in importance during November, but through the winter the use of legume seeds increased to as much as 62 percent by February. In the dark clay "black belt" acorns were not important, and legume seeds contributed over half of the November through February foods. In the red soils of the Piedmont and the red limestone valley soils of northern Alabama legume seeds also provided more than half of the food by volume.

To the west and north, the importance of cultivated grains and weedy herbaceous plants becomes more evident. In Texas, important winter foods

in the six different regions varies somewhat, but in four of these regions doveweeds (*Croton* spp.) are most important, and they are among the top five food sources in the other two regions. Danglepod (*Sesbania*) and panic grass (*Panicum*) were the primary food sources in these two regions but had reduced importance elsewhere (Principal game birds and mammals of Texas, 1945).

Winter foods of major importance in Oklahoma include weedy herbs such as ragweed (*Ambrosia*), sunflower (*Helianthus*), and trailing wild bean (*Strophostyles*), as well as acorns and cultivated plants such as sorghums and lespedezas, judging from various studies summarized by Rosene. Robinson's study of Kansas bobwhites (1957) indicated that during a nine-month period three plants, sorghum, wild beans, and foxtail millet (*Setaria*), were most important, and all of these were eaten during most of the nine months.

In Missouri, fall and winter foods vary in different regions, but on a state-wide basis the five most important seed-producing plants are probably Korean lespedeza, corn, ragweed, sorghum, and oats (Korschgen, 1948).

In the northern parts of the bobwhite's range, especially the "corn belt," the availability of corn or other grain is clearly of some importance for winter survival. In Nebraska corn is perhaps the most important winter food (Damon, 1949), and in Indiana the four most important fall foods were corn, sassafras, Korean lespedeza, and ragweed (Reeves, cited by Rosene, 1969). Winter foods in southern Illinois include, in diminishing importance by volume, corn, soybeans, Korean and common lespedeza, acorns and wheat (Larimer, 1960).

Bobwhites typically have two foraging sessions a day, one in early morning and one in late afternoon which lasts until dark. Little if any feeding is done when the vegetation is wet following rain or heavy dew, and the birds move only as far from their roosting cover as is needed to obtain adequate food. Birds of a covey feed together without aggression, and males may attract their mates to a choice morsel of food by using the tidbitting display. Grit may be picked up at the time of foraging, or searched out separately along roadways or cuts.

MOBILITY AND MOVEMENTS

Bobwhites are among the most sedentary of quails, and virtually no major seasonal movements are normally performed. Some early records of "migrations" were no doubt the result of dispersals following unusually high fall populations (Rosene, 1969). Perhaps the nearest approach to a true migration may be seen in the Smoky Mountains, where, at elevations

of from 3,500 to 6,500 feet, bobwhites occur on "grass balds" during the summer but are rare or absent there from September through April, when they move to lower grounds (Stupka, 1963).

During the winter covey period, each covey occupies a range which is large enough to fulfill its roosting, foraging, and escape-cover requirements but which rarely exceeds 50 acres. Rosene (1969) estimated the covey ranges of more than one thousand coveys in Alabama and South Carolina and found averages in four areas that ranged from 8.2 to 17.9 acres. Farther west and north the winter covey ranges may tend to be somewhat larger; Schemnitz (1961) summarized studies from Missouri and Texas that indicated an average winter covey range of 24 acres, and one from Oklahoma reported an average covey range of almost 50 acres. Robinson (1957) believed that a minimum of 12 acres was required to support a covey of bobwhites during the critical season in Kansas.

With the coming of spring, coveys gradually move from their winter range into the nesting range. In some areas, particularly in the south, these movements may not be very great. In one Kentucky study (Wunz, cited in Rosene, 1969), six of nine coveys moved less than one-quarter of a mile between late winter and early spring, and none moved more than three-quarters of a mile. Of thirty-four birds, twenty-four moved less than one-quarter of a mile. Similarly, in Florida all but one of twenty birds moved less than one-quarter mile between April 1 and mid-June (Loveless, 1958), and in Missouri most quail move less than one-half mile during the spring period (Murphy and Baskett, 1952).

In one Wisconsin study (Kabat and Thompson, 1963), movements of marked quail observed between April 8 and May 26 averaged 0.6 miles from the winter range, while between May 27 and June 23 the average distance for marked birds was 1.3 miles from the winter range. This would indicate that a considerable number of birds, perhaps unmated males, continue to move about for some time after the breakup of coveys. Robinson (1957) noted that movements of males during the breeding season were almost twice as far as during the nonbreeding season, with females' movements averaging only slightly less than those of males and the difference between yearling and adult birds being insignificant.

Summer movements by mated pairs and pairs with broods are relatively negligible. Studies of summer mobility in Missouri (Murphy and Baskett, 1952) and in Florida (Loveless, 1958) indicate that nearly 90 percent of the birds moved less than half a mile. In both instances, records of longer movements were believed to have been the result of movements of unmated males.

By fall, with the growth of the young completed, and the integration of

the broods into coveys, considerable social reorganization occurs. Unmated males and unsuccessful pairs probably attach themselves to pairs with well-grown young, and members of individual broods may break up and become affiliated with different fall coveys. This period of instability has been called the "fall shuffle." Agee (1957) investigated this phenomenon in Missouri and, surprisingly, found that fall movements (0.14 miles) averaged less than summer movements (0.39 miles) and were only somewhat greater than average winter movements (0.08 miles). He found that whistling males tended to join coveys near their summer ranges, with eleven of nineteen males apparently joined to the first family group they encountered. Of seven family groups, five had eventual winter ranges that overlapped their summer brood ranges, and a maximum movement of 200 yards was noted. Four fall coveys were developed from two families each plus unmated males and apparently unsuccessful pairs, while one covey was comprised of young from only one family. No quail in or with a brood moved more than 710 yards during the fall or winter, and most moved less than 400 yards.

In contrast to these findings, the studies of Duck (1943) indicate that in some areas fall movements may be considerable. In twelve or thirteen counties of northwestern Oklahoma, there is a distinct shift from summer ranges in sagebrush uplands and mixed grasslands to winter ranges in canyon bottoms and dunelands. Eleven quail that were banded during August and September and were recovered in December had moved an average distance of 9.7 miles and one was found 26 miles from the banding point, which is the maximum known case of a seasonal movement of bobwhites that I have encountered in the literature.

Yearly movements between successive winters provide a general index to bobwhite mobility traits; Kabat and Thompson (1963) noted that the average distance moved by both sexes between successive winters in Wisconsin was only 0.78 miles, with males moving significantly farther than females. In no case was a movement of more than four miles recorded among more than one hundred birds for which such records were obtained.

In summary, it would seem that in general bobwhites are not highly mobile, even during the fall period. Indeed, such mobility and potential range extension as does occur may be related more directly to late spring and summer movements by young birds, particularly males.

SOCIAL AND REPRODUCTIVE BEHAVIOR

During the winter the social unit is the covey, which as mentioned earlier tends to average from about 10 to 15 birds, largely because of the need for

efficient temperature maintenance during roosting. Kabat and Thompson (1963) noted that coveys drop in average size from about 17 birds in November to 7.5 birds by late March, representing a 56 percent winter loss. Other studies indicate covey sizes of from about 12 to 15 birds as typical, suggesting that covey size is a reflection of behavior rather than a possible index of population density. There appears to be no definite indication of specific age or sex structure in these winter coveys; males or females may predominate, and the size of the covey bears no apparent relationship to its age composition.

With spring, however, social structuring of the covey begins to develop. Rosene (1969) considered the breeding period to begin with the first *bobwhite* whistling, which may be as early as January in the South and early March in the northern states. However, if the bobwhite is like the western quails, much pair formation will have occurred before whistling is well under way. Further, it is most unlikely that pair formation under natural conditions is normally characterized by the male's performance of the elaborate display described by Stoddard (1931). However, his description is worth quoting, since it is the typical posture elicited when a male in breeding condition is initially exposed to either a strange female or male: "The display is a frontal one. The head is lowered and frequently turned sideways to show the snowy-white head markings to the best advantage, the wings are extended until the primary tips touch the ground, while the elbows are elevated over the back and thrown forward, forming a vertical feathered wall. The bird, otherwise puffed out to the utmost in addition to the spread, forward-thrust wings and lowered, side-turned head, now walks or advances in short rushes toward the hen, and follows her at good speed in full display in case she turns and runs." I have never seen the head-turning described by Stoddard, but otherwise his description agrees with my own observations. The similar if not identical responses of males to other males clearly indicates the aggressive nature of this display and its probable function in initial establishment of social dominance. Males in the same cage will not hold this posture long, but rather engage in actual fighting if they are roughly equal in social rank, but when prevented from fighting by cage walls will often perform the display whenever they are allowed to see one another.

Stokes (1967) has studied this "frontal" display and concluded that its function is aggressive rather than sexual, serving to establish social dominance. Only when a female fails to respond in kind does a male accept her as a female. Strictly sexual displays of the male bobwhite include lateral display, bowing, and tidbitting. During lateral display the male walks slowly about the female, with tail fanned and its upper surface tilted toward

her. The flank feathers are held loosely and drooped toward the ground and the head is somewhat lowered, but the wings are not distinctly drooped. Lateral display is silent and is usually brief. Bowing is closely associated with lateral display and consists of incomplete pecking movements, while the body is held horizontally and the bird walks around the female. During the breeding season the food call of the male is used in conjunction with pecking movements, which collectively serve as a tidbitting display and attract females, especially the male's mate. Tidbitting probably serves as a major means of pair bond maintenance, since it extends well beyond the period of actual pair formation. Female displays include wing-quivering movements and an inconspicuous lateral presentation display. Copulation is not preceded by any specific precopulatory behavior but is often preceded by female presentation behavior and is initiated by crouching on the part of the female. The female calls during copulation, but no definite postcopulatory display is present (Stokes, 1967).

Nest-building, performed by both sexes, is initiated by the digging of a scrape a few inches deep and four or five inches in diameter (Rosene, 1969). This scrape is then filled with dead leafy materials, so that the bottom of the nest is nearly level with the adjacent soil. Grasses or other herbaceous plants are arched over the top of the completed nest, effectively concealing it. The first egg is usually deposited one or two days later, and the egg-laying rate is approximately 1 per day with about eighteen to twenty days needed to complete a clutch of about 14 eggs. The average clutch size has been variously reported as 14.4 (Stoddard, 1931), 12.5 (Schemnitz, 1964), and 13.2 (Klimstra and Scott, 1957). There may be yearly variations in this, and in addition late clutches tend to have fewer eggs than do early-season clutches (Stoddard, 1931). Hatching typically occurs on the twenty-third day after incubation is initiated.

Robinson's study (1957) indicated that in Kansas during 1952 some nesting attempts were begun in early April or mid-April, while male calling did not become common until late May and early June, so that there was a lag of about a month between the peaks of nesting activity and calling. Peak calling occurred in mid-June, which was near the period (late June) Robinson estimated to be the time of maximum hatching. Fatora, Provost, and Jenkins (1967) also noted that male calling reaches a peak about a week before hatching. Robinson thought that "in addition to unmated males, mated males whistle in the breeding season, especially at the time of emergence of the young." However, Stoddard (1931) concluded that the whistle is "largely" that of unmated males, while Rosene (1969) thought that mated males "may or may not" whistle while the female is on the nest. Perhaps the best answer to this question comes from Robeson (1963), who compared the

whistling behavior of a definitely unmated male and an apparently mated male. He found that the unmated male usually uttered six or more calls per minute and called from eight to ten minutes, with the last note of the *ah-bob-white* call being loud and piercing. The bird almost always responded to a whistled covey call and was highly mobile, moving up to one-quarter mile in three hours. By contrast, the apparently mated bird called four or less times a minute, for durations of two minutes or less, and the last note of the call was soft and subdued. It was not observed to respond to the covey call, and was wholly sedentary.

From these and other reports, it would seem that nearly all the calling by male bobwhites is attributable to unmated birds that are announcing the locations of their whistling territories. These birds tend to establish such territories as close as possible to those of mated pairs, thus accounting for the positive relationship between the locations of calling males and nesting sites (Klimstra, 1950a). Such males with established whistling territories forceably expel other males from the immediate area and these nonterritorial birds, presumably most often yearlings, are no doubt responsible for the considerable summer movements recorded among males. In all likelihood, males which fertilized their mates early in the breeding season will have been past the peak of their fertility by the latter part of the female's incubation period. Should her nest be destroyed at that time, the availability of "surplus" whistling males still in maximum breeding condition makes a rapid remating and initiation of a fertile second clutch highly likely. Such a possibility would seem to provide the adaptive function of unmated males' whistling and more than counterbalance the potentially dangerous effect that their conspicuous presence near active nests might provide. The rapid decline in whistling at or shortly before the time of hatching probably is an indication that these birds are passing out of their reproductive condition. The gonadal cycle may be somewhat independent of the molt cycle as to hormonal control (Watson, 1962c), but it is probable that mated males would be first to go out of reproductive condition. At least in the case of males that have been participating in incubation (which may be about 25 percent of the nests judging from Stoddard's data), prolactin levels are undoubtedly high (Jones, 1969a). The birds' abilities for further gamete production are as a result probably quite limited, since high prolactin levels have been found to interfere with sperm production in such birds as phalaropes and white-crowned sparrows.

It is typical for females to renest at least once if their first attempt is unsuccessful, and perhaps as many as two or even three renesting attempts may be made. However, not only are renests somewhat smaller in average clutch size, but also the likelihood of successful hatching declines during

summer (Rosene, 1969). There is so far no indication that bobwhites ever normally have second broods under natural conditions, but in a captive situation three different pairs were observed to produce a second brood by the male's undertaking brooding responsibilities when the young were about two weeks old, and the female's then starting a second clutch (Stanford, 1953). It is possible that such behavior also occurs in wild populations where there is an unusually long breeding season, such as in Mexico, but this situation would be unlikely over most of the United States bobwhite range.

Although nesting losses may on the average be as high as 60 or 70 percent, persistent renesting attempts by females is likely to result in at least half of the adult females in a population bringing off a brood. Hatchability of eggs is usually high, and in Wisconsin and Iowa the initial brood size may be between 13 and 16 chicks (Klimstra, 1950b; Kabat and Thompson, 1963). Most chick mortality probably occurs during the first two weeks, and by late October and November the average brood size may be reduced to about 8.5. By that time the broods have been joined by unmated males and unsuccessful pairs, and the resulting fall coveys will have grown to about 12 to 17 birds. Fall age ratios in hunter-kill samples may range from as high as 85 percent juveniles (6.6 young per adult) to as low as 72 percent juveniles (2.4 young per adult), judging from a survey by Kabat and Thompson (1963). In general, about 80 percent of the fall population can be expected to consist of juvenile birds, which figure thus also roughly corresponds to the average annual mortality rate of the species. The resultant life expectancy for a bobwhite is less than a year; therefore relatively few birds survive to breed more than once.

Vocal Signals

The recent paper by Stokes (1967) provides a complete summary of the vocalizations of the bobwhite, which are perhaps the most diverse and complex of those of any United States species of quail.

The bobwhite call, already mentioned, is limited almost exclusively to males during the breeding season, particularly unmated ones.

Group movement calls used by both sexes are a series of increasingly louder *hoy, hoy-poo,* and *koi-lee* or *hoyee* notes that have been called the separation call (Stokes, 1967), scatter call, and covey call (Stoddard, 1931). Stokes has established that it not only functions to reunite separated pairs but also probably serves to space coveys, to attract unmated males to unmated females, and to repel intruders. Softer contact notes, *took* and *pitoo,* are used when the birds are feeding together. However, the typical

food-finding call is a soft *tu-tu-tu-tu* series of notes uttered with the bill pointed toward the source of food. This is used both by the male during the tidbitting display and by parents directing young to food.

When frightened by ground predators, a soft, musical *tirree* is initially uttered, but this usually quickly changes to an *ick-ick-ick* or *toil-ick-ick* as the birds become more alarmed. These latter notes are similar and no doubt correspond to the repeated *pit* or *chip* notes of *Callipepla* species. As the source of danger disappears, a soft *tee-wa* note may be uttered. The avian alarm note is a throaty *errrk*, and a loud, down-slurred distress *c-i-e-w* is produced when the birds are held in the hand. A somewhat similar but softer *psieu* note is uttered by adults during distraction display, which may be followed by repeated, staccato *tip* notes. Females may utter a "take-cover" call when a brood is disturbed, causing them to hide and freeze.

Agonistic calls of the bobwhite are greater in number than those of *Callipepla;* Stokes has recognized four different calls functioning in this situation. These are the "caterwaul," *squee, hoy,* and *hoy-poo.* Of these, only the caterwaul and *squee* are limited to the agonistic situation, while the *hoy* and *hoy-poo* have group and pair contact functions as well. Both caterwauling and the *squee* may be performed by both sexes but are more frequent in males. The *squee* note, a long series of whining or muttering-like sounds, is indicative of a thwarted attack or a balance between attack and escape tendencies. The caterwaul, however, is a loud, raucous call sounding like *h-a-o p-o-o w-e-i-h'* that is clearly indicative of a dominant status and a strong attack tendency and is often associated with frontal display. Rarely do males utter this call toward strange females, but it is typically elicited when a strange pair is visible, and less often when a single rival male is seen. Its nearest functional equivalent in *Callipepla* is the head-throw of the scaled quail or the *squill* of the California quail, although the associated postures and sounds are quite different from either of these.

Stokes has mentioned several additional calls typical of parent-young interactions, including a "broody call" of the parents, two different alarm notes, as well as the "take cover," distraction, or "decoy ruse" call, and the food-finding calls already mentioned. Chicks have at least two calls, a "contentment" note and a distress or separation call.

EVOLUTIONARY RELATIONSHIPS

There can be little doubt that the nearest living relatives of *Colinus* are the species of *Callipepla (sensu lato).* Holman (1961) has indicated that on the basis of skeletal structure these species might be considered congeneric, and I (1970) have indicated that the same conclusion might be made on the

basis of hybridization evidence. Were it not for the taxonomic problems at the species level existing within the bobwhites, this would probably be the best treatment, but considering that three fairly distinct populations of bobwhites exist and at least for the present are best regarded as full species, the application of the generic name *Colinus* to this population complex seems the most practical method of emphasizing their close relationships to one another without too seriously obscuring the relationships of the bobwhite group to the more typically crested quails of the arid Southwest.

Among the *Colinus* × *Callipepla* hybrids so far produced (involving Gambel, California, and scaled quails), only those with one California quail parent have exhibited any fertility beyond the F_1 generation so that second generation (F_2) hybrids have been hatched and have survived to maturity. It seems reasonable to believe that the ancestral *Colinus* type diverged from an ancestral *Callipepla* well before any splitting of the latter's gene pools into populations representative of any of the living species. The southernmost point of current common contact between the genera is southern Mexico, and this area would seem to be a possible region of origin for the genus *Colinus*. Possibly the Isthmus of Tehuantepec served as an initial extrinsic isolating factor that split the early *Colinus* population into northern (pre-*virginianus*) and southern (pre-*cristatus, nigrogularis*) segments, or perhaps the mountainous highlands of northwestern Guatemala provided such a barrier, but at least at present the latter group of mountains seems to be the primary barrier between the *insignis* population of *virginianus* and the *incanus* population of *cristatus* (see figure 41). Curiously, no such major barrier separates the coastal populations of *virginianus salvini* and *cristatus hypoleucus*, which are presently separated only by about three hundred kilometers of Guatemala coastal plain between Chiapas and El Salvador.

Assuming that *Colinus* originated in the area of what is now interior Chiapas, the pre-*virginianus* stock probably followed river systems northward to the coastal plain of the Caribbean, where it then moved northward along the Gulf Coast ultimately reaching what is now the eastern half of the United States, where its northward expansion was ultimately limited by cold winters and its western limits set by the arid climates and resulting absence of woody vegetation. The birds also dispersed from the Chiapas highlands to the Pacific coast of Mexico, and northwestward along that coastline in savanna or similar habitats until blocked from further expansion by the arid coastal desert of Sonora, with the interior Sonoran masked bobwhite population representing the point of maximal northwestern expansion. This population was evidently subsequently isolated from the other black-throated and coastal-dwelling populations by extinction of populations between Sinaloa and Guerrero. The Valley of Mexico and ad-

joining temperate uplands were likewise colonized, probably through movement upward along river systems draining into the adjacent Gulf coastal plains. There birds exhibit the white-throated and fairly light-bodied characteristics of the Atlantic coastal populations, rather than the black-headed and generally dark-bodied condition typical of Pacific coastal birds and those of the Chiapas highlands.

South of the Guatemalan highlands, the ancestral *Colinus* stock probably followed coastal plains and arid highlands southward and eastward, perhaps initially giving rise to a Caribbean coastal population that subsequently developed into *nigrogularis*, as well as a series of more southerly populations that ultimately crossed the Panama Isthmus and spread out over a considerable portion of northern South America. For reasons not presently clear, these populations acquired (or more probably retained) a more distinctly crested condition in males than did those occurring farther north, but this is of minor taxonomic importance. Local adaptations also modified the degree of body darkness, especially the amounts of brown and yellow feather pigments. Maximal loss of pigmentation occurred in the arid Guatemala highlands and adjacent El Salvador, while many of the more southerly populations acquired a fairly dark coloration.